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Tolerance of understory plants subject to herbivory by roe deer

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Current understanding of plant–herbivore interactions postulates that forest understory species are less tolerant to herbivory by large mammals than grassland species. As yet, research on forest species has focused on extensive biomass loss. However, forest dwelling ungulates are often selective browsers, hence biomass loss experienced by forage species is mostly limited to specific plant modules. We investigated the impact of herbivory on common forage species of roe deer *Capreolus capreolus* by simulating browsing on wild transplants of the two herbs *Geum urbanum* and *Prenanthes purpurea,* and the two graminoids *Carex sylvatica* and *Luzula luzuloides.* Two clipping regimes simulated different browsing frequencies, whereas shading and full day light represented light conditions in closed forests and gaps, respectively. Single clipping did not affect above ground biomass production of any species, independent of light conditions. Repeated biomass loss led to undercompensation in *L. luzuloides,* marginal compensation in *C. sylvatica,* and full compensation in *G. urbanum* and *P. purpurea* measured as above ground biomass production. The change in root biomass after clipping was positively correlated with the change in above ground biomass production in all four species. In contrast, nitrogen concentration was negatively correlated with above ground biomass in the graminoids, whereas no relationship between nitrogen and biomass was found in the herbs. Although light conditions and plant provenance affected biomass production, we found no effect of light conditions on plant reactions to herbivory. These results suggest that forest understory species, graminoids as well as herbs, are tolerant to herbivory by selective browsers such as roe deer. As in grassland ecosystems, the degree of compensatory growth depends on amount and frequency of biomass loss.

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Structure and composition of plant communities are known to be influenced by large herbivores (Hobbs 1996, Putman 1996). Differences in tolerance to herbivory can alter the competitive relationships among co-occurring plants and may thus lead to changes in the abundance of individual species (Coughenour 1985, Augustine and McNaughton 1998). Tolerance can involve various mechanisms that allow plants to cope with herbivore damage, e.g. compensatory growth, storage and relocation of nutrients, regulation of photosynthetic activity, or release of apical dominance (Strauss and Agrawal 1999, Tiffin 2000). Compensation of biomass lost to herbivory has been found in many species from tropical to arctic grasslands. At moderate grazing intensities and high nutrient input some species are even able to increase primary productivity (McNaughton 1979, Georgiadis et al. 1989, De Mazancourt et al. 1998). In contrast to grassland species, understory species of temperate forests are considered less tolerant to herbivory (Gill 1992, Kirby 2001, Rooney and Waller 2003). Several studies in Great Britain and northern America found that forest herbs

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decreased at high deer densities, while grasses and sedges increased. However, reactions of understory species to moderate herbivory are largely unknown (Whitham et al. 1991, Juenger and Lennartsson 2001). Browsing ungulates are often very selective with respect to plant tissue so that large parts of their food plants remain undamaged (Hofmann 1989). As deer are an integral part of temperate forest ecosystems, we suggest that tolerance to moderate herbivory should be widespread among common and palatable understory species.

In deciduous lowland forests of northern Switzerland, roe deer *Capreolus capreolus* L. are the principal and often the only large herbivore. They feed on a variety of understory species, herbs as well as graminoids (Klötzli 1965, Duncan et al. 1998). Herbaceous species and graminoids are likely to react differently to herbivory because of differences in morphology and growth characteristics (Haukioja and Koricheva 2000). Furthermore, they are browsed or grazed in different seasons, thus different phenological stages are subjected to herbivory (Klötzli 1965, B. Moser, unpubl.). Plant reactions do not only depend on morphology and timing of herbivory but also on environmental conditions such as light, nutrient and water supply (Maschinski and Whitham 1989, Edenius 1993, Cronin and Lodge 2003). So far, only few investigations have been made into the importance of light for tolerance and biomass compensation (Strauss and Agrawal 1999). In contrast to grassland ecosystems, forest understory species are generally light limited (Coughenour 1985). However, canopy disturbances and subsequent changes in light conditions are recurrent in forests – be it due to management measures or natural forces like windthrow. As light affects plant growth, morphology, and resource allocation of plants, light conditions are likely to influence plant responses to herbivory (Whitham et al. 1991).

The aim of this study was to assess the capacity of common understory species to tolerate herbivory by roe deer. Tolerance was measured as the species' ability to compensate for the biomass lost to herbivory, e.g. by producing new biomass or increasing vegetative production. We tested the hypotheses that (1) common forest understory species would be able to compensate single biomass loss in terms of biomass production, (2) compensation would decline with increasing browsing frequency, (3) biomass compensation would be lower under shady conditions than in full daylight (closed forest vs gap), and (4) plants would decrease nitrogen content of above ground biomass with increasing browsing frequency.

The impact of browsing was investigated on two forest herbs – *Geum urbanum* L. and *Prenanthes purpurea* L. – and two forest graminoids – *Carex sylvatica* Hudson and *Luzula luzuloides* (Lam.) Dandy et Wilmott. As environmental factors and clipping frequency are difficult to control in field experiments, the study was carried out by means of a common garden experiment on wild transplants (Tiffin and Inouye 2000, Bergström and Edenius 2003).

Material and methods

Plant material

All studied species are known to be frequently browsed or grazed by roe deer in temperate deciduous forests of northern Switzerland (Klötzli 1965). *Geum urbanum* is a clonal, perennial herb which essentially occurs in moderate shade of woodland, scrub and hedgerows, but can also be found in more open disturbed habitats (Taylor 1997). *Prenanthes purpurea* is also clonal and perennial and grows in forests with rich herb layer or in tall forb communities (Sell 1976, Hess et al. 1980). In northern Switzerland, inflorescences and fruits of *G. urbanum* and *P. purpurea* are mainly browsed in summer with a peak between June and July (Klötzli 1965). The sedge *Carex sylvatica* and the rush *Luzula luzuloides* typically occur in deciduous forests and grow in tussocks (Hess et al. 1980). Leaves of *C. sylvatica* and *L. luzuloides* are mainly grazed early in the year, between February and April, whereas inflorescences and fruits are not generally used (Klötzli 1965).

Individual rosettes of *G. urbanum,* rhizomes of *P. purpurea* and tussocks of *C. sylvatica* and *L. luzuloides* were collected from eight spatially independent forest stands (provenances) in northern Switzerland in October 2001 (Table 1). The forest stands are dominated either by beech (*Fagus sylvatica* L.) or spruce (*Picea abies* L.), the two most common tree species in Switzerland. Grazing history, local environmental conditions as well as genetic predisposition may affect susceptibility of an individual plant to herbivory. As these factors are difficult to measure and mostly unknown, we chose plants of different provenance in order to obtain results that are valid for a range of forest stands. The tussocks of *C. sylvatica* and *L. luzuloides* were divided into groups of 3–5 (C. *sylvatica*) and 8–9 (*L. luzuloides*) tillers, respectively. The wild plants were transplanted into individual plastic pots filled with a mixture of wood fibre, humus, and peat supplemented by a long-term fertiliser (3 g Osmocote plus (16% N, 8% P, 12% K) per litre substratum), which corresponds to rich forest soils. The pots were placed in an experimental field at WSL in Birmensdorf (northern Switzerland). In order to prevent water deficiency, plants were watered during long rainless periods. Herbivorous invertebrates were eliminated by a single application of a wide-spectrum insecticide (Phosdrin, Agroplant; May 2002) and by spreading molluscide pellets (Limax, Maag; May and July 2002).

Table 1. Provenance of plant material used in the clipping experiment: coordinates, altitude (meters above sea level), and dominating tree species of the forest sites.

	Coordinates		Altitude	Main tree species	*C. sylvatica*	*G. urbanum*	*L. luzuloides*	*P. purpurea*
a. Birmensdorf ZH	47°22′ N	8°27′ E	550	*Fagus sylvatica*	x	x		
b. Frutigen BE	46°34′ N	7°38′ E	850	*Picea abies*				x
c. Giswil OW (Rinderalp)	46°50′ N	8°06′ E	1350	*Picea abies*				x
d. Giswil OW (Stockmatt)	46°49′ N	8°08′ E	1200	*Picea abies*				x
e. Habsburg AG	47°28′ N	8°12′ E	400	*Fagus sylvatica*	x	x	x	
f. Hönggerberg ZH	47°25′ N	8°30′ E	520	*Fagus sylvatica*	x	x		
g. Kandersteg BE	46°31′ N	7°40′ E	1000	*Picea abies*				x
h. Müntschemier BE	47°01′ N	7°10′ E	450	*Fagus sylvatica*	x	x	x	

Experimental design and protocol

The experiment was laid out in a modified split-split-plot design. The layout comprised two main blocks (whole-plots) and three sub-blocks nested within each treatment level of the main blocks. The main block treatment was light, i.e. half of each main block was shaded, whereas the rest was exposed to full daylight. Each of the 12 sub-blocks contained 12 plants of each species with the treatment combinations of the factors provenance (4 levels) and clipping (3 levels), hence the experiment included a total of 144 plants per species. In the case of *L. luzuloides* each treatment combination occurred twice per sub-block because plants originated from only two sites instead of four (Table 1). Sub-block, position within sub-blocks, and treatment combination were randomly assigned to individual plants.

Main blocks and sub-blocks were designed to control between-block and within-block variation, respectively, whereas the factors clipping, light and provenance were used to simulate herbivory under varying environmental conditions. The factor light comprised two treatment levels: full daylight, simulating gaps, and shading with wooden slats (2 cm wide, 1 cm apart, 130 cm above ground). The slats were designed to simulate the migration of sunny spots on the forest floor providing individual plants with short periods of direct sunlight. Additionally to the slats, shading cloths were fixed on the southern side of the sub-blocks.

Shading was set up at the beginning of April when beech trees in the surrounding forests came into leaves. There were three levels of clipping: no clipping (control), clipping once, and clipping twice. Clipping treatments were designed to simulate natural browsing or grazing by roe deer as closely as possible (Table 2). For the herbs, treatments were defined according to the description of roe deer feeding habits by Klötzli (1965). As for *L. luzuloides,* the natural level of grazing was determined by measuring the height of 60 grazed tussocks in a beech forest in Habsburg, Switzerland, in February 2002. Mean height of grazing was found to be at 5.0 cm (±0.6 SE) above soil level. Shoots of *C. sylvatica* were also clipped at 5 cm above soil level. The amount of biomass removed and the dates of clipping are listed in Table 2. Clipping was executed manually.

Plants were harvested shortly before seed dispersal, i.e. at the beginning of July with *C. sylvatica* and *L. luzuloides,* and at the end of August with *G. urbanum* and *P. purpurea,* respectively. Plants were divided into above ground and below ground (root) biomass, and roots were subsequently cleaned from soil under running water. In order to investigate the changes in nutrient content of the plant parts that might be reconsumed by roe deer, above ground biomass of *G. urbanum* and *P. purpurea* was further separated into main and lateral shoots, whereas shoots of *C. sylvatica* and *L. luzuloides* were divided into biomass below and above 5 cm above soil level, respectively (cf. clipping treatments Table 2). All plant parts were weighed after drying in an oven at 60°C for 48 h (*C. sylvatica, L. luzuloides, P. purpurea*) and 72 h (*G. urbanum*), respectively. Shoot tissue >5 cm of *C. sylvatica* and *L. luzuloides,* and lateral shoots of *G. urbanum* and *P. purpurea* were ground with a Retsch MM 2000 ball mill and analysed for concentrations of nitrogen and carbon. Nitrogen and carbon analyses were done by the laboratory of the Swiss Federal Research Institute WSL (accredited according to ISO17025) on Carlo Erba NA-1500 and CE-Instruments NC-2500 analysers.

Data analysis

Effects of clipping on biomass and nutrient content of plants were analysed by analysis of variance (ANOVA). ANOVA was done for each species separately using the univariate general linear model procedure of SPSS (Release 11.0.1, SPSS Inc., Chicago 2001). The factors included in the analysis were main block, sub-block, light, provenance and clipping. Main blocks and sub-blocks were considered random factors. Since randomisation of the whole-plot factors is not complete in a split-split-plot design, the factors light and main block were tested against their interaction (whole-plot error), the other factors were tested against the residuals (Sahai and Ageel 2000). As there were only two main blocks (whole-plot replicates), differences between treatment levels of the factor light were rarely significant. If light had nevertheless very large mean square and F-values compared to the other factors, the ANOVA model was

Table 2. Clipping treatments applied to plant species. *C. sylvatica* and *L. luzuloides:* all shoots >5 cm were clipped at 5 cm above soil level. *G. urbanum*: main shoots were clipped right underneath the leaf that encompasses the lowest flowering stalk having a minimum length of 5 cm, lateral shoots were clipped 2 cm from main shoot. *P. purpurea*: main shoots were clipped at half shoot length, lateral shoots 2 cm from main shoot.

	Treatment	Removed plant parts	Clipping date
C. sylvatica	1st clipping	shoots	13.–15.03.2002
	2nd clipping	shoots	25.04.2002
	harvest (incl. control)	whole plant	09.–11.07.2002
L. luzuloides	1st clipping	shoots	13.–15.03.2002
	2nd clipping	shoots	25.04.2002
	harvest (incl.control)	whole plant	01.–03.07.2002
G. urbanum	1st clipping	main shoots with inflorescences	14.06.2002
	2nd clipping	lateral shoots	15.–16.07.2002
	harvest (incl. control)	whole plant	19.–21.08.2002
P. purpurea	1st clipping	main shoots with inflorescences	25.06.2002
	2nd clipping	lateral shoots	25.07.2002
	harvest (incl. control)	whole plant	26.–27.08.2002

adjusted by neglecting the main blocks. In this case light was tested against sub-blocks nested within light. The adjusted ANOVA model was based on the assumption that the main blocks were similar in regard to environmental factors such as soil fertility, light conditions, and water supply. In cases where data did not meet assumptions of normality or homogeneity of variances, logarithmic or square root transformation improved data structure satisfactorily. Because interpretation of results was not affected by transformation, untransformed data are presented. Tukey HSD test was used for multiple comparisons among treatment levels. The relationship between above ground biomass production and root biomass, and between above ground biomass and nitrogen content was analysed by regression analysis using function lm of the statistical computing system R version 1.7.1 (R Development Core Team 2005).

Results

Effect of clipping

Single clipping did not affect above ground biomass production (ABP; sum of total above ground biomass produced up to harvest) in the graminoids (Fig. 1) nor in the herbs (Fig. 2). All species compensated for the biomass lost to clipping independent of light conditions (Table 3). In *G. urbanum,* overcompensation was found in once clipped plants grown in full daylight of two sites (Birmensdorf: $P = 0.023$; Hoenggerberg: $P = 0.047$). *G. urbanum* and *P. purpurea* were also able to compensate repeated biomass loss. However, we found only marginal compensation following two clippings in *C. sylvatica,* as indicated by the low P-value of the clipping treatment (Table 3), and undercompensation in *L. luzuloides.* While root biomass of *C. sylvatica* and *P. purpurea* was not affected by clipping, twice-clipped plants of *G. urbanum* had larger roots than once-clipped and unclipped plants. In contrast, root biomass of *L. luzuloides* decreased with clipping. In all species, the change in root biomass after clipping (once and twice) was positively correlated with the change in ABP (Fig. 3). Concentration of nitrogen was not affected by single clipping in *C. sylvatica, L. luzuloides* and *P. purpurea,* but it was higher in twice-clipped than in unclipped plants. Conversely, nitrogen concentration in *G. urbanum* decreased both in once and twice clipped plants. In *C. sylvatica* and *L. luzuloides,* nitrogen concentration was negatively correlated with above ground biomass, whereas no relationship was found in *G. urbanum* and *P. purpurea* (Fig. 4). C/N-ratio was strongly negatively correlated with nitrogen content, independent of species, clipping treatment, light conditions and provenance ($R^2 > 0.87$; $P < 0.0001$).

Effect of light and provenance

Light conditions affected biomass production and nutrient allocation, but not plant reactions to clipping. In all species, plants grown in full daylight had higher root biomass than shaded plants (Fig. 1, 2). *C. sylvatica* and *L. luzuloides* also produced more above ground biomass in full daylight than in the shade, whereas light had no effect on ABP of *G. urbanum* and *P. purpurea.* Nitrogen concentration was higher in shaded plants than in plants grown in full daylight in both graminoids as well as in *G. urbanum,* whereas no effect of light was found in *P. purpurea.* ABP and root biomass further differed between plants of different provenance (Fig. 1, 2), except for root biomass of *G. urbanum* (Table 3). In contrast, nitrogen concentration was not affected by plant provenance. Reactions of plants to clipping were for the most part independent of provenance. Significant interactions were found between provenance and clipping in root biomass of *L. luzuloides* (Fig. 1), and between provenance, light and clipping in ABP of *G. urbanum* (Fig. 2), i.e. plants of different provenance did not react uniformly to the clipping and light treatments, respectively.

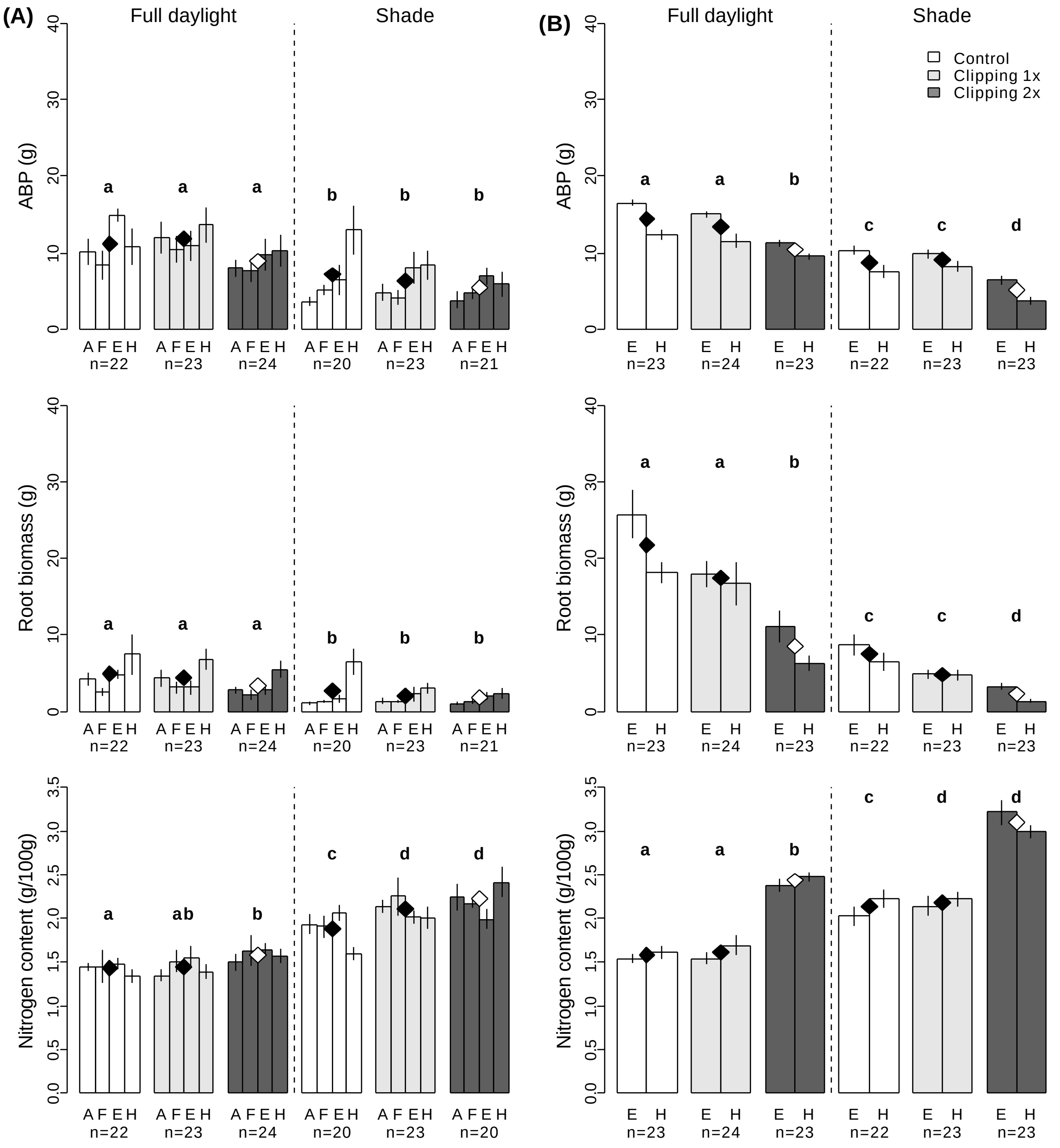

Fig. 1. Effects of clipping on above ground biomass production (ABP), root biomass at the time of harvest, and nitrogen concentration of shoot tissue >5 cm at the time of harvest in plants of the two understory graminoids (A) *C. sylvatica* and (B) *L. luzuloides* grown in full daylight and shade, respectively. Bars represent means of single provenances (±SE), black and white diamonds represent means of all provenances. Different letters above diamonds indicate significant differences between overall means (Tukey's HSD, $p < 0.05$). Provenances, indicated by capital letters, as in Table 1.

Discussion

Plant responses to herbivory are very variable. They can differ between ecosystems and species but also within species (Milchunas and Lauenroth 1993, Danell and Bergström 2002). Investigations into the impact of herbivory on forest understory species showed that severe defoliation can lead to biomass undercompensation in several perennial forest herbs (see summary in Rooney and Waller 2001). However, complete defoliation, as simulated in these studies, does not correspond to the foraging behaviour of roe deer, the most common large herbivore in deciduous forests of northern Switzerland. Roe deer are very selective with respect to plant tissue, thus plants are rarely fully defoliated (Klötzli 1965, B. Moser, pers. obs.). Similarly to studies in

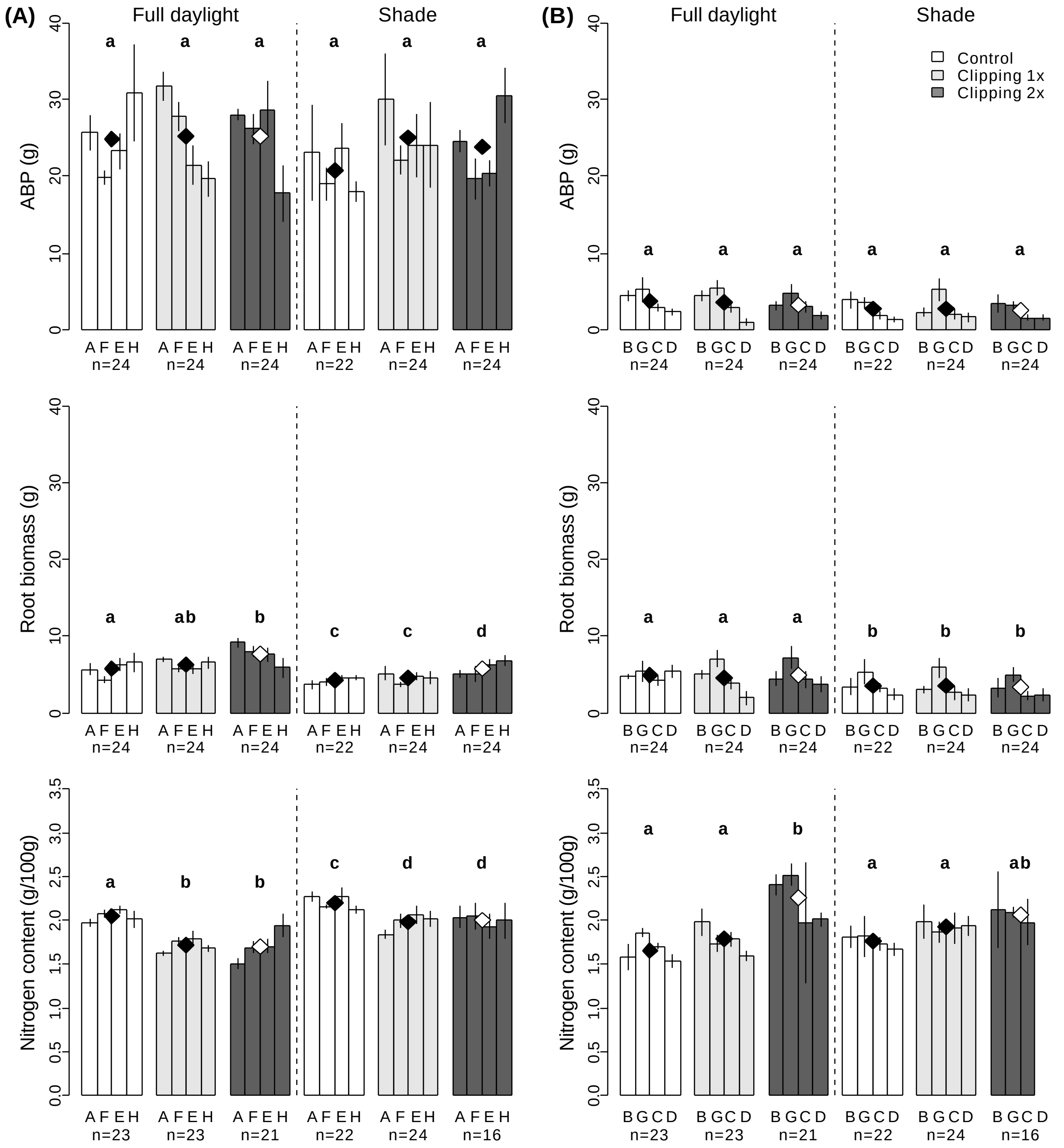

Fig. 2. Effects of clipping on above ground biomass production (ABP), root biomass at the time of harvest, and nitrogen concentration of lateral shoots at the time of harvest in plants of the two understory herbs (A) *G. urbanum* and (B) *P. purpurea* grown in full daylight and shade, respectively. Bars represent means of single provenances ($\pm$SE), black and white diamonds represent means of all provenances. Different letters above diamonds indicate significant differences between overall means (Tukey's HSD, $p < 0.05$). Provenances, indicated by capital letters, as in Table 1.

grassland ecosystems, where biomass compensation mainly occurs at moderate grazing intensities (Georgiadis et al. 1989, De Mazancourt et al. 1998, Huhta et al. 2003), we found that single clipping did not affect short-term ABP of the studied forest herbs and grasses. Even after two consecutive clippings, the herbs *G. urbanum* and *P. purpurea* were able to compensate for the biomass loss. Consequently, common understory species are more tolerant to herbivory than assumed up to now. Their reactions seem to depend on amount and frequency of biomass loss, as reactions of species in grassland ecosystems do (Fox et al. 1998, Huhta et al. 2003).

Herbs in general, and forest herbs in particular, have been considered less tolerant to herbivory than graminoids (Haukioja and Koricheva 2000, Rooney and Waller 2003). It has been argued that morphology

Table 3. Results of analysis of variance (split-split-plot) on the effects of light and clipping on above ground biomass production (g), root biomass at the time of harvest (g), and nitrogen concentration of above ground biomass (shoot tissue >5 cm in graminoids, lateral shoots >2 cm in herbs) at the time of harvest (g/100 g dry matter) for the two graminoids (A) *C. sylvatica* and (B) *L. luzuloides,* and the two herbs (C) *G. urbanum* and (D) *P. purpurea.* Significant results ($P < 0.05$) are displayed in bold font.

Source of variation	Above ground biomass production			Root biomass			Nitrogen concentration		
	F	df	P	F	df	P	F	df	P
A. Light	29.609	1,4	**0.006**	549.858	1,1	**0.036**	144.843	1,4	**0.000**
Main block				2.160	1,1	0.380			
Main block × light					1				
Subblock (light)		4						4	
Subblock (main block × light)				1.039	8,99	0.413			
Provenance	5.193	3,105	**0.002**	9.912	3,99	**0.000**	0.756	3,104	0.521
Clipping	2.657	2,105	0.075	1.974	2,99	0.144	8.242	2,104	**0.000**
Light × provenance	1.164	3,105	0.327	1.319	3,99	0.273	0.823	3,104	0.484
Light × clipping	0.340	2,105	0.712	0.128	2,99	0.880	1.769	2,104	0.176
Provenance × clipping	0.284	6,105	0.943	0.346	6,99	0.911	1.565	6,104	0.165
Light × provenance × clipping	1.456	6,105	0.200	0.921	6,99	0.483	1.156	6,104	0.336
Error		105			99			104	
B. Light	199.900	1,4	**0.000**	133.841	1,4	**0.000**	168.161	1,4	**0.000**
Subblock (light)		4			4			4	
Provenance	53.908	1,122	**0.000**	20.623	1,122	**0.000**	1.419	1,122	0.236
Clipping	44.012	2,122	**0.000**	59.693	2,122	**0.000**	125.251	2,122	**0.000**
Light × provenance	1.036	1,122	0.311	0.231	1,122	0.632	0.630	1,122	0.429
Light × clipping	1.099	2,122	0.337	0.422	2,122	0.657	0.521	2,122	0.595
Provenance × clipping	1.129	2,122	0.327	4.123	2,122	**0.019**	1.324	2,122	0.270
Light × provenance × clipping	1.445	2,122	0.240	0.484	2,122	0.617	1.370	2,122	0.258
Error		122			122			122	
C. Light	0.787	1,1	0.538	495.056	1,1	**0.029**	71.733	1,4	**0.001**
Main block	6.022	1,1	0.246	0.986	1,1	0.502			
Main block × light		1			1				
Subblock (light)								4	
Subblock (main block × light)	0.837	8,108	0.572	1.365	8,108	0.220			
Provenance	2.871	3,108	**0.040**	1.468	3,108	0.227	1.665	3,101	0.179
Clipping	0.927	2,108	0.399	10.042	2,108	**0.000**	28.009	2,101	**0.000**
Light × provenance	0.883	3,108	0.452	1.523	3,108	0.213	1.178	3,101	0.322
Light × clipping	0.685	2,108	0.506	0.112	2,108	0.894	1.273	2,101	0.284
Provenance × clipping	1.091	6,108	0.372	0.670	6,108	0.674	1.196	6,101	0.315
Light × provenance × clipping	3.467	6,108	**0.004**	1.889	6,108	0.089	1.179	6,101	0.323
Error		108			108			101	
D. Light	1.634	1,1	0.422	118.959	1,4	**0.000**	0.127	1,1	0.776
Main block	1.568	1,1	0.429				0.967	1,1	0.505
Main block × light		1						1	
Subblock (light)					4				
Subblock (main block × light)	0.640	8,98	0.742				0.783	8,72	0.619
Provenance	13.212	3,98	**0.000**	9.952	3,104	**0.000**	2.484	3,72	0.067
Clipping	0.306	2,98	0.737	0.252	2,104	0.778	11.444	2,72	**0.000**
Light × provenance	0.417	3,98	0.741	0.047	3,104	0.986	0.372	3,72	0.774
Light × clipping	0.155	2,98	0.856	0.416	2,104	0.661	1.819	2,72	0.169
Provenance × clipping	0.532	6,98	0.783	0.654	6,104	0.687	0.800	6,72	0.573
Light × provenance × clipping	0.660	6,98	0.682	0.676	6,104	0.669	0.418	5,72	0.835
Error		98			104			72	

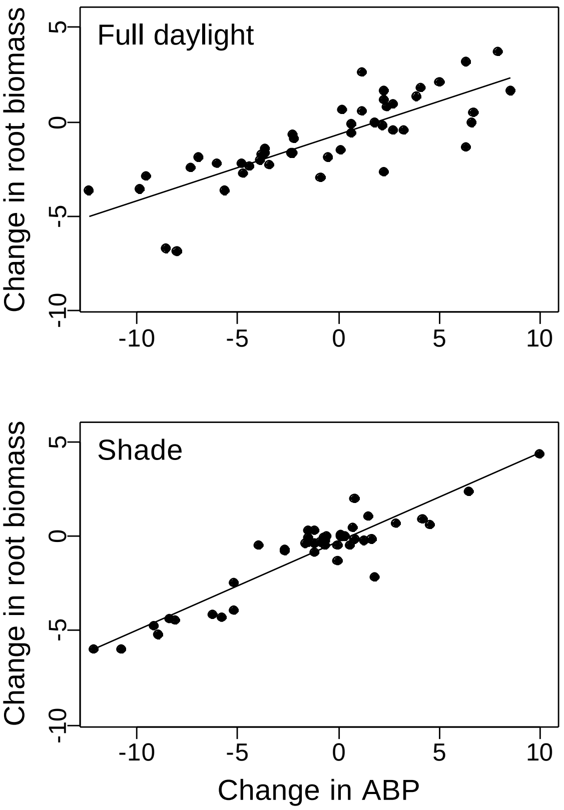

Fig. 3. Change in above ground biomass production (ABP) compared to the change in root biomass after clipping in plants of *C. sylvatica* grown in full daylight ($y = -0.671 + 0.351x$, $R^2 = 0.761$, $p < 0.0001$; $n = 69$) and shade ($y = -0.263 + 0.471x$, $R^2 = 0.721$, $p < 0.0001$; $n = 64$), respectively.

facilitated regrowth in graminoids. As growth takes place from basal meristems, which are protected from herbivory, regrowth can start immediately after damage without activation of new meristems (Haukioja and Koricheva 2000). Timing of roe deer herbivory also seems to benefit graminoids since it occurs early in the year, and early season herbivory has been considered easier to compensate for than late season herbivory (Whitham et al. 1991, Strauss and Agrawal 1999). Contrary to these predictions, we found no difference in reactions to single clipping between graminoids and herbs, whereas repeated clipping negatively affected biomass production in the graminoids. Maybe graminoids are not prepared for such late herbivory as in our experiment. Besides morphology and timing of herbivory, the ability to relocate resources between plant modules has been considered crucial for a species' capacity to tolerate herbivory (Whitham et al. 1991, Haukioja and Koricheva 2000). In our experiment, the change in root biomass after clipping was positively correlated with the change in ABP both in the herbs as well as in the graminoids. This indicates that plants adjusted biomass allocation so as to restore initial root/shoot ratio, although restoration was not complete. Similar trends in restoration of root/shoot ratio have been found in a wide range of species, herbs as well as graminoids (Brouwer 1962, Farrar and Gunn 1998, Poorter and Nagel 2000). Evidence for resource relocation was also found in terms of nitrogen. In the herbs, changes in nitrogen concentration seems to depend directly on clipping, as nitrogen was not related to above ground biomass. In contrast, nitrogen concentration was inversely proportional to above ground biomass in graminoids. Thus, changes in nitrogen may simply be a consequence of the changes in biomass in these species (Koricheva 1999). Alternatively, elevated nitrogen content after clipping may not be the result of relocation but of increased nitrogen uptake. Irrespective of the underlying mechanisms, the differences in nitrogen concentration between unclipped and clipped plants may have important consequences for resource selection by roe deer as nitrogen seems to be positively correlated with food quality for this herbivore (Tixier et al. 1997, Duncan et al. 1998). While *G. urbanum* may prevent rebrowsing by decreasing nitrogen concentration after herbivory, the graminoids and *P. purpurea* seem to enhance the nutritional quality of the regrown tissue. The attractiveness of a plant to herbivores does not only depend on its nutritional quality but also on its palatability, which may decrease after herbivory if plants increase the concentration of chemical defensive compounds (Karban and Baldwin 1997, Danell and Bergström 2002). However, joint effects of defensive compounds and nutrients on herbivores are still poorly understood (Villalba et al. 2002), and studies on the impact of defensive compounds on diet selection of roe deer are controversial (Verheyden-Tixier and Duncan 2000, Clauss et al. 2003). Improvement of food quality after herbivory was also found in grassland ecosystems and in some deciduous trees (Coughenour 1991, Ouellet et al. 1994, Fox et al. 1998). So called 'grazing lawns', where grazed patches are more often used by herbivores than ungrazed patches (McNaughton 1984, Hobbs et al. 1991, Schütz et al. 2003), led to the hypothesis that herbivores can manage their food resources in order to benefit from the responses at a later time (Danell and Bergström 2002). Our findings suggest that active management of understory graminoids by roe deer is unlikely on the time scale of a growing season, because food quality only improved after two consecutive clippings. Feeding loops over one or more years have not been studied in forest understory species yet, but were found in birch in temperate forests of northern Europe. Moose *Alces alces* (L.) preferred trees of *Betula pendula* and *B. pubescens* that were browsed in the previous season over unbrowsed trees (Danell et al. 1985).

Plant reactions to browsing do not only depend on plant characteristics and feeding behaviour of herbivores, but also on environmental conditions and plant

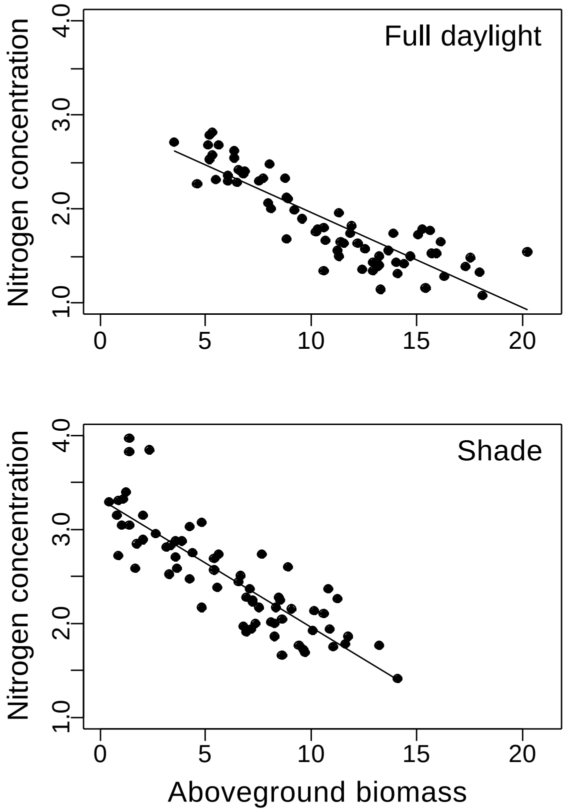

Fig. 4. Relationship between nitrogen concentration (g/100 g dry matter) of shoots >5 cm and above ground biomass (g) at the time of harvest in plants of *L. luzuloides* grown in full daylight ($y = 2.976 - 0.102x$, $R^2 = 0.665$, $p < 0.0001$; $n = 70$) and shade ($y = 3.307 - 0.135x$, $R^2 = 0.881$, $p < 0.0001$; $n = 68$), respectively.

provenance (Whitham et al. 1991, Strauss and Agrawal 1999). Provenance may influence tolerance of individual plants to herbivory because of differences in grazing history or genetic predisposition. While provenance affected ABP of all species, increase in light enhanced ABP only in the graminoids. As susceptibility to herbivory has been found to be related to plant productivity in several graminoids but also in the birch *B. pendula* and in Scots pine *Pinus sylvestris* (Edenius et al. 1995, Buckland and Grime 2000, Ylioja et al. 2000), we expected plant provenance and light conditions to interact with plant responses to clipping. However, interactions were only found with root biomass of *L. luzuloides* (provenance × clipping) and ABP of *G. urbanum* (light × provenance × clipping). Light conditions did not only influence ABP but also nitrogen content of the shoot tissue. The higher nitrogen concentration in shaded plants of *C. sylvatica, L. luzuloides* and *G. urbanum* in comparison to plants growing in full daylight may have important consequences for habitat use by foraging roe deer. Forest gaps have long been considered attractive to herbivores because of abundant forage (Happe et al. 1990, Senn et al. 2002). In contrast, several studies found the quality of woody forage to be lower in gaps than in mature forests, both because of lower nitrogen concentration and higher tannin content (Bunnell and Jones 1984, Van Horne et al. 1988, Happe et al. 1990). Our results indicate that this does not only apply for woody species but also for graminoids and herbs. Since many forest dwelling ungulates are so called concentrate selectors, which depend on high quality food (in cervidae e.g. roe deer, white-tailed deer *Odocoileus virginianus* (Zimmermann, 1780), or moose; Hofmann 1989), improvement of habitat for these deer species should involve preservation of mature forest stands rather than creation of forest gaps.

Our results indicate that there might be a mutualistic relationship between forest dwelling roe deer and palatable understory species. On the one hand, selective foraging seems to preserve the quantity of available food resources, because understory plants are adapted to a feeding behaviour which leaves large parts of the plant undamaged. On the other hand, understory species appear to produce high quality food under shady conditions, which in turn enables forest dwelling ungulates to be selective feeders with respect to plant tissue. Since our study was a pot experiment and covered only a short period of time compared to the lifespan of the studied species, long-term field studies would be welcome to reinforce these results.

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